# REPRODUCTIVE SUCCESS OF PIPING PLOVERS AT BIG QUILL LAKE, SASKATCHEWAN

## WAYNE C. HARRIS,<sup>1,6</sup> DAVID C. DUNCAN,<sup>2,3,7</sup> RENEE J. FRANKEN,<sup>3</sup> DONALD T. MCKINNON,<sup>2,5</sup> AND HEATHER A. DUNDAS<sup>4</sup>

ABSTRACT .- Big Quill Lake, Saskatchewan, is an important breeding area for Piping Plovers (Charadrius melodus); the area hosts up to 8% of the continental breeding population, yet little is known about how the site contributes to the overall survival of this species. We studied the reproductive success of Piping Plovers at Big Quill Lake from 1993 to 1995. We located 208 nests and captured and banded 456 young. Nest initiation occurred from mid-May to mid-July, and median nest-initiation dates were 14, 13, and 13 May in 1993, 1994, and 1995, respectively. Mean clutch size for presumed first nests was 3.92 eggs. Nesting success was consistently high from 1993 to 1995, with Mayfield estimates of nest success ranging from 75 to 88%; nests initiated later in the season were less successful than earlier nests. The wide beach (200-1,000 m) at Big Quill Lake may have contributed to high nesting success by reducing efficiency of predators. Use of Big Quill Lake beaches by humans and cattle was also minimal. Fledging success varied dramatically, with 0.02, 1.35, and 1.78 young fledged per breeding pair in 1993, 1994, and 1995, respectively. Low productivity of Piping Plovers in 1993 was a result of low chick survival during a week of rain, cold temperatures, and high winds, rather than low nesting success. Fledging success in 1994 and 1995 was higher than the 1.24 chicks per pair required for population stability on alkaline lakes in the Northern Great Plains. This high productivity suggests that Big Quill Lake is an important Piping Plover breeding site and measures should be taken to ensure its continued protection. Received 21 April 2004, accepted 3 March 2005.

Piping Plover (Charadrius melodus) numbers have declined continentally in the last 50 years, due in part to permanent destruction of breeding and wintering habitats, and reduced reproductive success (Sidle 1984, Haig 1992). This decline has resulted in the Piping Plover being listed as an endangered species in Canada (Haig 1985), endangered in the Great Lakes region of the United States, and threatened elsewhere in the United States (Sidle 1984). Low reproductive success is considered a limiting factor to the recovery of Piping Plovers in the Northern Great Plains (Haig 1992, Ryan et al. 1993, Murphy et al. 1999); however, this aspect of demography has been documented at relatively few alkali lakes (Haig and Plissner 1992, Plissner and Haig

Dave.Duncan@ec.gc.ca

1997, Murphy et al. 1999). Monitoring reproductive success is considered a priority for the recovery of this species (U.S. Fish and Wildlife Service 1994).

Factors thought to affect reproductive success of Piping Plovers include weather (e.g., Grover and Knopf 1982, Haig and Oring 1988, Sidle et al. 1992), fluctuating water levels (e.g., Mayer i990, Sidle et al. 1992, Espie et al. 1998, Skeel and Duncan 1998), and egg and chick predation (e.g., Rimmer and Deblinger 1990, Mayer and Ryan 1991, Melvin et al. 1992, Mabee and Estelle 2000). The importance of these factors can vary annually and with the type of breeding site (Larson et al. 2002).

Big Quill Lake, Saskatchewan, is a large alkaline wetland and is an important breeding site for Piping Plovers in North America. In 1996, the site had the largest breeding population (435 birds) of any site in North America—8% of the continental population and 26% of the Canadian prairie population (Skeel et al. 1997). However, numbers fluctuate widely from year-to-year: the last three International Censuses at Big Quill Lake reported 151 adults in 1991 (Haig and Plissner 1992), 435 adults in 1996 (Plissner and Haig 1997), and 105 adults in 2001 (Ferland and Haig 2002); Harris and Lamont (1991) reported 43

<sup>&</sup>lt;sup>1</sup> Prairie Environmental Services, Box 414, Raymore, SK S0A 3J0, Canada.

<sup>&</sup>lt;sup>2</sup> Saskatchewan Wetland Conservation Corp., 110– 2151 Scarth St., Regina, SK S4P 3Z3, Canada.

<sup>&</sup>lt;sup>3</sup> Current address: Canadian Wildlife Service, Room 200, 4999–98 Avc., Edmonton, AB T6B 2X3, Canada.

<sup>&</sup>lt;sup>4</sup> 14 Arnheim Rd., Whitehorse, YT Y1A 3B4, Canada.

<sup>&</sup>lt;sup>5</sup> Current address: Saskatchewan Environment, 3211 Albert St., Regina, SK S4S 5W6, Canada.

<sup>&</sup>lt;sup>6</sup> Deceased.

<sup>&</sup>lt;sup>7</sup> Corresponding author; e-mail:

birds in 1989, and Harris estimated over 440 birds in 1995 (W. C. Harris pers. comm. *in* Skeel et al. 1997).

Even though Big Quill Lake can support a large breeding population of Piping Plovers, there is very little information on Piping Plover reproductive success at this lake and the role it plays in the overall conservation of this species. The purpose of this paper is to examine the reproductive success of Piping Plovers at Big Quill Lake by documenting nesting chronology, nesting success, and fledging success. Knowledge of Piping Plover reproductive success at such an important breeding area will increase our ability to conserve and manage this endangered species.

## METHODS

Study area.—Big Quill Lake (51° 53' N, 104° 15' W) is a large (30,700 ha), shallow, saline basin on the Central Saskatchewan Plains about 200 km east of Saskatoon. The shoreline is primarily alkaline mudflats, and is approximately 200 km long when the basin is full. The upper beaches are partially to fully vegetated with alkali grass (Distichlis stricta), western sea-blite (Suaeda depressa), Nuttall's salt-meadow grass (Puccinellia nuttalliana), northern reed grass (Calamagrostis inexpansa), and wild barley (Hordeum jubatum). In 1993 and 1994, the basin was approximately 60% flooded, and beach width was approximately 1,000 m (Harris 1993, 1994). In 1995, the water level in Big Quill increased due to heavy snowfall the previous winter, resulting in a beach width of <200 m (Harris 1995).

Nest surveys.—Our study area was located on the east side of Big Quill Lake and composed approximately one-third of the shoreline. During 1993–1995, we surveyed the study area at least twice weekly from 7 May to 30 August. We searched for territorial pairs of Piping Plovers (birds calling, exhibiting aggressive or defensive behavior, or performing courtship displays) by systematically walking or slowly traversing the shoreline with an allterrain vehicle (ATV). We watched territorial birds from a distance of 50-100 m, which allowed birds to return to their nest. We plotted the location of all birds on a map of the study area. We marked nests with pin-flags placed at least 30 m away in the adjacent vegetation, and plotted nest locations on an aerial photo-

graph of the shore. We determined nest occupancy using a  $15-60 \times$  telescope from a distance of 50-100 m during repeat visits. We visited nests every 3 days during initiation and early incubation. Most nests were located during egg-laying; when full clutches were found, a single egg was floated to estimate incubation stage (Schwalbach 1988). We estimated hatch dates assuming a 6-day egg-laying period and a 28-day incubation period (Whyte 1985). We used this information to return to nests near hatching and band chicks before they moved away from their nest. Although young plovers generally left the nest scrape shortly after the last egg hatched, they were rarely far from the scrape during the first few days, and the broods remained close to their nest site until they were capable of flight.

Chicks were banded with a standard federal aluminum leg band, and either one or two colored celluloid bands to allow for further recognition without recapture. Color-banded broods were checked every 2 to 3 days to monitor survival and movements, and all nests and broods were followed until fledging or nest failure. Young that disappeared after they reached 21 days of age were considered to have fledged (Haig 1992). We defined fledging rate as the number of young fledged per breeding pair. Murphy et al. (1999) suggest that fledging rate is the most important measure of reproductive success for the Piping Plover, because it represents "a direct link to recruitment." We defined the number of breeding pairs as the number of first nests. We distinguished first nests from late nests based on break points in nest-initiation dates, and assumed that late nests were renests. Between mid-July and mid-August, we made weekly visits to six staging areas located outside the study area to check for marked young that may have been alive but missed during surveys of the study area.

Statistical analysis.—We used the Mayfield method to estimate nesting success (Mayfield 1961, 1975). Nests were considered successful if at least one chick hatched. Mayfield nest success was defined as  $(1 - \text{daily mortality rate})^N$ , where daily mortality rate = number of nest losses/total exposure days, and N = nesting period. The average nesting period from nest initiation (first egg) to hatching (first hatch) was 33 days. We also estimated egg

| Productivity variable                                     | 1993                    | 1994                        | 1995                  |
|---|-------------------------|-----------------------------|-----------------------|
| Median nest-initiation date                               | 14 May                  | 13 May                      | 13 May                |
| (range)   | (10 May-11 July)        | (10 May-21 June)            | (10 May-21 June)      |
| Number of nests   | 51                      | 73                          | 84                    |
| Number of first nests <sup>a</sup> (and presumed renests) | 42 (9)                  | 71 (2)                      | 83 (1)                |
| Number of eggs laid (mean $\pm$ SE)                       | $183 (3.59 \pm 0.12)$   | $280 (3.84 \pm 0.06)$       | $333 (3.96 \pm 0.00)$ |
| Number of chicks hatched (mean $\pm$ SE)                  | $144 \ (2.82 \pm 0.24)$ | $231 \ (3.16 \ \pm \ 0.18)$ | $287 (3.42 \pm 0.15)$ |
| Number of chicks fledged (mean $\pm$ SE)                  | $1 (0.02 \pm 0.02)$     | 96 (1.32 ± 0.17)            | 148 (1.76 $\pm$ 0.16) |
| Daily survival rate of nests<br>(DSR) <sup>b</sup>        | 0.991                   | 0.994                       | 0.996                 |
| Mayfield nest success<br>(95% CI) <sup>c</sup>            | 0.752 (0.63–0.89)       | 0.822 (0.73-0.92)           | 0.875 (0.80–0.95)     |

TABLE 1. Nesting chronology, clutch size, and reproductive success of Piping Plovers at Big Quill Lake, Saskatchewan, 1993-1995.

<sup>a</sup> First nests were distinguished from renests based on a break point in nest-initiation dates. Nests initiated after 27 June, 20 June, and 20 June for 1993, 1994, and 1995, respectively, were considered renests.

<sup>6</sup> Mayfield nest success = DSR<sup>33</sup> (33 is the calculated average nesting period from nest initiation [first egg] to hatching); SE = {[DSR(1 - DSR)]/total exposure days}<sup>1/2</sup>; 95% Confidence Limits =  $[DSR \pm 2(SE)]^{32}$ 

success (proportion of eggs that hatched) and fledging success (mean number of fledglings per breeding pair).

We used Cox regression survival analysis to examine the effect of year on survival of broods. The Cox proportional hazards model (Cox 1972) models the hazard rate or the rate of failure. The hazard rate is assumed to be a function of time, but this method does not attempt to characterize the function (Nur et al. 2004). The null hypothesis is that the ratio of hazard rates = 1 (i.e., no difference between groups). Survival analysis includes time-todeath and time-to-end-of-monitoring data for broods that were still alive when monitoring ceased. Survival analysis is useful when the ultimate outcome may be uncertain (i.e., when it is not possible to continue monitoring nests due either to weather or the culmination of the nesting cycle). For our study, we were certain how long broods survived, but only until monitoring ceased. Data are considered to be right-censored when the start time is known, but (brood) failure time is unknown. Our data were right-censored because there was incomplete information on the outcome (i.e., we do not know when all individuals died). We defined survival time as time from hatch to the last day chicks were observed. Chicks were assumed to have died if they disappeared before 21 days of age. As long as one chick in each brood survived to the end of monitoring, the brood was still considered to be alive. We compared brood survival for 1993 to 1995 and 1994 to 1995.

We used the Kruskal-Wallis rank sum test to determine whether nest-initiation data varied among years, and we used linear regression to determine whether clutch size decreased with nest initiation. We used logistic regression to determine whether nest and fledging success-both measured as binary response variables (1 = success, 0 = failure) were dependent on nest-initiation date (all nests combined). We used S-PLUS (Mathsoft, Inc. 1997) to conduct statistical analyses. Means are presented  $\pm$  SE.

#### RESULTS

Nest chronology.-We found 208 nests and captured and banded 456 young on the east side of the lake (Table 1). We banded 140 of 148 hatched young in 1993, 129 of 232 in 1994, and 187 of 288 in 1995.

Egg-laying commenced by the 2nd week in May and continued until the 2nd week in July. Over half of all nests were initiated in a 4-day period from 11 to 14 May. The median date of nest initiation was 14, 13, and 13 May in 1993, 1994, and 1995, respectively, and did

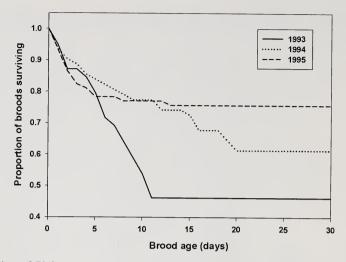


FIG. 1. Proportion of Piping Plover broods surviving (presumed) from hatching to fledging at Big Quill Lake, Saskatchewan, 1993–1995. Chicks that disappeared after 21 days were assumed to have fledged.

not differ among years (Kruskal-Wallis  $\chi^2 = 0.52$ , df = 2, P = 0.77, n = 208). However, in 1993, 18% (n = 9) of nests were initiated after 26 June, whereas in 1994 and 1995, no nests were initiated after this date.

We estimated 42, 71, and 83 breeding pairs in 1993, 1994, and 1995, respectively, based on the estimated number of first nests. In 1993, no nests were initiated between 2 and 26 June; thus, we assumed that the nine nests initiated after 26 June were renests. In 1994, no nests were initiated between 14 and 20 June and the two nests initiated after 20 June were considered renests. In 1995, no nests were initiated between 14 and 20 June and we assumed that the single nest initiated on 21 June was a renest.

Clutch size.—Mean clutch size was 3.92 ± 0.02 eggs/clutch for presumed first nests and  $2.25 \pm 0.28$  eggs/clutch for late nests (all years combined). Clutch size decreased with nest-initiation date (linear regression:  $\beta$  = -0.035, SE = 0.002,  $F_{1,207}$  = 461.27, P <0.001). Late nests had a mean of 1.89  $\pm$  0.2 (n = 9),  $3 \pm 1$  (n = 2), and 4 (n = 1) eggs per nest in 1993, 1994, and 1995, respectively. Of 51 nests initiated in 1993, 2% (n = 1) had five eggs, 75% (n = 38) had four eggs, 8% (n = 4) had three eggs, 12% (n = 6) had two eggs, and 4% (n = 2) had one egg. In 1994, of 73 nests initiated, 88% (n = 64) had four eggs, 8% (n = 6) had three eggs, and 4% (n= 3) had two eggs. Of 84 nests initiated in

1995, 1% (n = 1) had five eggs, 94% (n = 79) had four eggs, and 5% (n = 4) had three eggs.

Nesting success, fledging success, and brood survival.---Mayfield nest success was high in all years (75, 82, and 88% in 1993, 1994, and 1995, respectively). The probability of nesting success decreased with later nestinitiation dates (logistic regression:  $\beta$  = -0.040, SE = 0.012, t = -3.50, df = 1, P <0.001). One percent (n = 1), 42% (n = 96), and 52% (n = 148) of chicks fledged in 1993, 1994, and 1995, respectively. In 1993, 0.02 young fledged per breeding pair, whereas in 1994 and 1995 fledgling success was 1.35 and 1.78 per pair. Nests with later hatch dates had lower fledging success (logistic regression: ß = -0.047, SE = 0.017, t = -2.85, df = 1, P = 0.001). Brood survival was lower in 1993 than in 1995 (Z = 3.45, P < 0.001), but was not significantly different between 1994 and 1995 (Z = 1.73, P = 0.084; Fig. 1).

#### DISCUSSION

Median nest-initiation dates in this study were similar to those found at Big Quill Lake in 1980 and 1981 (13 May and 9 May; Whyte 1985), and at Lake Diefenbaker, Saskatchewan (e.g., 12 May in 1992 and 9 May 1993; Espie et al. 1998). However, the 1993 nesting attempts at Big Quill Lake were the latest reported in over 10 years of monitoring, and no young fledged from those nests (Harris 1993). Harris (1993) attributed the late nesting to large losses of nests and broods in early spring during a period of inclement weather. Piping Plovers can renest once or twice in a season if the eggs are destroyed, and there are records of them producing two broods in a year (Bottitta et al. 1997); however, usually they raise only one brood per year (Haig 1992).

A seasonal decline in clutch size and reproductive success has been well documented for birds in general (e.g., Lack 1968, Klomp 1970, Perrins 1970, Daan et al. 1989), and Piping Plovers in particular (Knetter et al. 2002). We found a similar pattern of larger clutch sizes and greater hatching success in early nests. We also found that clutch sizes of Piping Plovers at Big Quill Lake were similar to those reported from other studies (Haig 1992). The smaller average clutch sizes in 1993 were likely the result of a large renesting effort. Declines in reproductive success over a season are thought to be related to physiological or energy demands related to timing of breeding (Lepage et al. 1999), or to lower quality or fitness of later breeders (Verhulst et al. 1995).

Mayfield nest success was consistently high from 1993 to 1995 and was greater than nest success estimates from other sites (e.g., Mayer and Ryan 1991, Patterson et al. 1991, Loegering and Fraser 1995, Mabee and Estelle 2000, Lauro and Tanacredi 2002). Several factors may explain the high nest success at Big Quill Lake from 1993 to 1995. First, predation pressure at Big Quill Lake may be lower than at other lakes in the region due to the relatively wide shoreline, which lowers the probability of predators detecting nests (Prindiville Gaines and Ryan 1988, Espie et al. 1996). Even though we observed a dramatic change in the average distance from nesting sites to water from 1994 to 1995, productivity changed little between these years, suggesting that beach width in 1995 (200 m) was still above the minimum threshold required for good nesting success. In fact, productivity was slightly higher in 1995, when the beach was narrower, suggesting that even when water levels are high at this lake, the distance from water to nesting sites, and/or from permanent vegetation to nest sites, may still be sufficient to allow for high nest and fledging success. In addition to the wide beach, there are few trees, shrubs, or other perch sites in proximity to the nesting areas around Big Quill Lake, which may have reduced perching opportunities for avian predators. Disturbance by humans and cattle was low at Big Quill Lake, but is known to reduce productivity in some areas (e.g., Burger 1994). Mayfield nest success estimates from our study, and from more recent studies at Big Quill Lake (2002–2004; C. Gratto-Trevor unpubl. data), also were greater than those recorded at Big Quill Lake in the early 1980s (16% and 29%, Whyte 1985); the reason for this difference is unknown.

Although Piping Plover nest success was high from 1993 to 1995, fledging success varied among years, which is typical of this species (Haig and Oring 1987, Maxson and Haws 2000, Knetter et al. 2002). At alkaline lakes in the Great Plains, Piping Plover reproductive success averages 0.89 fledglings per pair without predator exclusion, and 1.28-1.78 fledglings per pair with predator exclusion (Larson et al. 2002). Larson et al. (2002) determined that a mean reproductive success of 1.24 fledglings per pair would be required at alkaline lakes to stabilize a declining population of Piping Plovers. This target was exceeded in 1994 and 1995 at Big Quill Lake, and it was greater than Whyte's (1985) 0.76 fledglings per pair at Big Quill Lake a decade earlier (although the low reproductive success reported by Whyte [1985] was due, in large part, to a lower rate of nesting success as opposed to fledging success). The high reproductive success at Big Quill Lake during 1994 and 1995 suggests that-at least in some years-this area may serve as a source for Piping Plovers in the Northern Great Plains.

Low fledging success in 1993 may be due, in part, to a period of prolonged heavy rainfall, combined with cold temperatures and high winds (Harris 1993). Prior to 27 June, 55% of young were still alive, after which there was a long period of inclement weather. Once conditions had improved sufficiently to allow monitoring to resume on 7 July, all young and eggs had disappeared from the study area and a renesting effort was under way. The only chick that was known to have fledged in 1993 was later found at a staging area. It is probable, however, that other young fledged during this period of no monitoring, and were not accounted for at staging areas later in the season. Seventeen broods were 13–15 days old before monitoring temporarily ceased and some of these chicks may have fledged before monitoring resumed 9 days later. We feel that the low number of birds fledging in 1993 is likely an underestimate, although similarly low numbers of young Piping Plovers observed at the Big Quill Lake staging areas corroborates low fledging success in 1993. Survival analysis also suggests that brood survival was lower in 1993 than 1995, but was not different between 1994 and 1995, corroborating the low fledging success in 1993.

Our study suggests that Big Quill Lake may serve as a population source for Piping Plovers in the Great Plains. The low productivity of Piping Plovers at Big Quill Lake in some years may be a result of low chick survival rather than low nesting success. Because of the numbers of nesting pairs and recent high productivity, the importance of Big Quill Lake as a breeding area for Piping Plovers is evident. Measures should continue to ensure its protection and integrity.

## ACKNOWLEDGMENTS

We dedicate this paper to the memory of W. C. Harris, who was the primary investigator on this project along with help from field assistants A. Harris, V. Harris, S. Lamont, T. Lazorko, and S. McAdam. This research was funded by the Prairie Shores Program of the North American Waterfowl Management Plan as part of a study to assess habitat enhancement for Piping Plovers. The Canadian Wildlife Service funded the updated analyses presented here. Helpful comments were provided by S. Davis, J. P. Goossen, C. Gratto-Trevor, V. Harris, S. Lamont, S. J. Maxson, and two anonymous reviewers.

### LITERATURE CITED

- BOTTITTA, G. E., A. M. COLE, AND B. LAPIN. 1997. Piping Plovers produce two broods. Wilson Bulletin 109:337–339.
- BURGER, J. 1994. The effect of human disturbance on foraging behavior and habitat use in Piping Plover (*Charadrius melodus*). Estuaries 17:695–701.
- Cox, D. R. 1972. Regression models and life tables. Journal of the Royal Statistical Society, Series B 34:187–220.
- DAAN, S., C. DIJKSTRA, R. H. DRENT, AND T. MEIJER. 1989. Food supply and the annual timing of avian reproduction. Pages 392–407 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Sciences, Ottawa, Canada.

- ESPIE, R. H. M., R. M. BRIGHAM, AND P. C. JAMES. 1996. Habitat selection and clutch fate of Piping Plovers (*Charadrius melodus*) breeding at Lake Diefenbaker, Saskatchewan. Canadian Journal of Zoology 74:1069–1075.
- ESPIE, R. H. M., P. C. JAMES, AND R. M. BRIGHAM. 1998. The effects of flooding on Piping Plover *Charadrius melodus* reproductive success at Lake Diefenbaker, Saskatchewan, Canada. Biological Conservation 86:215–222.
- FERLAND, C. L. AND S. M. HAIG. 2002. 2001 International Piping Plover census. U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon.
- GROVER, P. B. AND F. L. KNOPF. 1982. Habitat requirements and breeding success of Charadriiform birds nesting at Salt Plains National Wildlife Refuge, Oklahoma. Journal of Field Ornithology 53: 139–148.
- HAIG, S. M. 1985. The status of the Piping Plover in Canada. Report to the Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ontario.
- HAIG, S. M. 1992. Piping Plover (*Charadrius melodus*). The Birds of North America, no. 2.
- HAIG, S. M. AND L. W. ORING. 1987. Population studies of Piping Plovers at Lake of the Woods, Minnesota, 1982–1987. Loon 59:113–117.
- HAIG, S. M. AND L. W. ORING. 1988. Mate, site, and territory fidelity in Piping Plovers. Auk 105:268– 277.
- HAIG, S. M. AND J. H. PLISSNER. 1992. 1991 International Piping Plover census. Report to U.S. Fish and Wildlife Service Region 3, Division of Endangered Species, Ft. Snelling, Minnesota.
- HARRIS, W. C. 1993. Piping Plover population evaluation at Big Quill Lake habitat enhancement study area—1993. Saskatchewan Wetland Conservation Corporation, Regina, Saskatchewan, Canada.
- HARRIS, W. C. 1994. Piping Plover population evaluation at Big Quill Lake habitat enhancement study area—1994. Saskatchewan Wetland Conservation Corporation, Regina, Saskatchewan, Canada.
- HARRIS, W. C. 1995. Piping Plover population evaluation at Big Quill Lake habitat enhancement study area—1995. Saskatchewan Wetland Conservation Corporation, Regina, Saskatchewan, Canada.
- HARRIS, W. C. AND S. M. LAMONT. 1991. Saskatchewan Piping Plover population assessment—1990: Big Quill Lake, Chaplin Lake, Lake Diefenbaker, Redberry Lake and the South Saskatchewan River (Gardiner Dam to Saskatoon). Saskatchewan Environmental Society, Saskatoon, Canada.
- KLOMP, H. 1970. The determination of clutch size in birds: a review. Ardea 58:1–124.
- KNETTER, J. M., R. S. LUTZ, J. R. CARY, AND R. K. MURPHY. 2002. A multi-scale investigation of Piping Plover productivity on Great Plains alkali lakes, 1994–2000. Wildlife Society Bulletin 30: 683–694.
- LACK, D. L. 1968. Ecological adaptations for breeding

in birds. Methuen Publishing, London, United Kingdom.

- LARSON, M. A., M. R. RYAN, AND R. K. MURPHY. 2002. Population viability of Piping Plovers: effects of predator exclusion. Journal of Wildlife Management 66:361–371.
- LAURO, B. AND J. TANACREDI. 2002. An estimation of predatory pressures on Piping Plovers nesting at Breezy Point, New York. Waterbirds 25:401–409.
- LEPAGE, D., A. DESROCHERS, AND G. GAUTHIER. 1999. Seasonal decline of growth and fledging success in Snow Geese Anser caerulescens: an effect of date or parental quality? Journal of Avian Biology 30:72–78.
- LOEGERING, J. P. AND J. D. FRASER. 1995. Factors affecting Piping Plover chick survival in different brood-rearing habitats. Journal of Wildlife Management 59:646–655.
- MABEE, T. J. AND V. B. ESTELLE. 2000. Assessing the effectiveness of predator exclosures for plovers. Wilson Bulletin 112:14–20.
- MATHSOFT, INC. 1997. S-PLUS 4 guide to statistics. Mathsoft, Inc. Seattle, Washington.
- MAXSON, S. J. AND K. V. HAWS. 2000. Population studies of Piping Plovers at Lake of the Woods, Minnesota: 19 year history of a declining population. Waterbirds 23:475–481.
- MAYER, P. M. 1990. Conservation biology of Piping Plovers in the Northern Great Plains. M.Sc. thesis, University of Missouri, Columbia.
- MAYER, P. M. AND M. R. RYAN. 1991. Survival rates of artificial Piping Plover nests in American Avocet colonies. Condor 93:753–755.
- MAYFIELD, H. F. 1961. Nest success calculated from exposure. Wilson Bulletin 73:255–261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.
- MELVIN, S. M., L. H. MACIVOR, AND C. R. GRIFFIN. 1992. Predator exclosures: a technique to reduce predation at Piping Plover nests. Wildlife Society Bulletin 20:143–148.
- MURPHY, R. K., B. G. ROOT, P. M. MAYER, J. P. GOOS-SEN, AND K. A. SMITH. 1999. A draft protocol for assessing Piping Plover reproductive success on Great Plains alkali lakes. Pages 90–107 *in* Proceedings, Piping Plovers and Least Terns of the Great Plains and nearby (K. F. Higgins, M. R. Brashier, and C. D. Kruse, Eds.). South Dakota State University, Brookings.
- NUR, N., A. L. HOLMES, AND G. R. GEUPEL. 2004. Use of survival time analysis to analyze nesting success in birds: an example using Loggerhead Shrikes. Condor 106:457–471.

- PATTERSON, M. E., J. D. FRASER, AND J. W. ROGGEN-BUCK. 1991. Factors affecting Piping Plover productivity on Assateague Island. Journal of Wildlife Management 55:525–531.
- PERRINS, C. M. 1970. Timing of birds' breeding seasons. Ibis 112:242–255.
- PLISSNER, J. H. AND S. M. HAIG. 1997. 1996 International Piping Plover census. U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon.
- PRINDIVILLE GAINES, E. AND M. RYAN. 1988. Piping Plover habitat use and reproductive success in North Dakota. Journal of Wildlife Management 52:266–273.
- RIMMER, D. W. AND R. D. DEBLINGER. 1990. Use of predator exclosures to protect Piping Plover nests. Journal of Field Ornithology 61:217–223.
- RYAN, M. R., B. G. ROOT, AND P. M. MAYER. 1993. Status of Piping Plovers in the Great Plains of North America: a demographic simulation model. Conservation Biology 7:581–585.
- SCHWALBACH, M. J. 1988. Conservation of Least Terns and Piping Plovers along the Missouri River and its major western tributaries in South Dakota. M.Sc. thesis, South Dakota State University, Brookings.
- SIDLE, J. G. 1984. Piping Plover proposed as an endangered and threatened species. Federal Register 49:44712–44715.
- SIDLE, J. G., D. E. CARLSON, E. M. KIRSCH, AND J. J. DINAN. 1992. Flooding: mortality and habitat renewal for Least Terns and Piping Plovers. Colonial Waterbirds 15:132–136.
- SKEEL, M. A. AND D. C. DUNCAN. 1998. Population size and productivity of Piping Plovers at Lake Diefenbaker in relation to water level. Blue Jay 56:137–146.
- SKEEL, M. A., D. C. DUNCAN, AND E. R. WILTSE. 1997. Saskatchewan results of the 1996 International Piping Plover census. Blue Jay 55:157–168.
- U.S. FISH AND WILDLIFE SERVICE. 1994. Draft revised recovery plan for Piping Plovers, *Charadrius melodus*, breeding on the Great Lakes and Northern Great Plains of the United States. Twin Cities, Minnesota.
- VERHULST, S. J., J. H. VAN BALEN, AND J. M. TINBER-GEN. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? Ecology 76:2392–2403.
- WITYTE, A. J. 1985. Breeding ecology of the Piping Plover (*Charadrius melodus*) in central Saskatchewan. M.Sc. thesis, University of Saskatchewan, Saskatoon, Canada.